

A COMPARATIVE DEVELOPMENTAL STUDY OF A DWARF MUTANT  
IN MAIZE, AND ITS BEARING ON THE INTERPRETATION  
OF TASSEL AND EAR STRUCTURE

S. G. STEPHENS

*Carnegie Institution of Washington, Department of Genetics,  
Cold Spring Harbor, Long Island, New York*<sup>1</sup>

The homologies of tassel and ear structure in maize, and the problem of the morphological relationship between the inflorescences of maize and other genera in the Gramineae, have provided a fascinating study for many workers. Mangelsdorf (1945) has lately compiled a critical review of the earlier contributions to these problems, and with the aid of more recent data has endeavored to formulate a hypothesis incorporating the main features of previous theories. It is interesting to note that most workers have considered the maize inflorescence (tassel or ear) as a unit for comparative study which is complete in itself. Anderson (1944) first realized the importance of considering the structure of the inflorescence as a culmination of developmental processes which are common to the plant as a whole. It would seem that a study of the inflorescence apart from the rest of the shoot might neglect a very valuable source of information, and that a better understanding of the general developmental plan in the maize plant might furnish a new line of attack in interpreting the particular morphology of the inflorescence.

Adopting this line of approach, the problem of ear and tassel homologies involves three ontogenetic questions:

(1) Bonnett (1940) showed that the primordia giving rise to lateral branches, and the primordia giving rise to paired spikelets on the main axis of the tassel, are homologous structures. Paired spikelets may therefore be regarded as greatly reduced lateral branches. Is this reduction peculiar to the tassel or is it the culmination of a process initiated during the vegetative phase?

(2) Mangelsdorf (1945) concluded that the ear of maize as exemplified by the female inflorescence of Guarany pod corn is "fundamentally identical with the spikes of certain other species of grasses . . . and like many of them is probably derived from a panicle as the result of reduction of branches. There is not the slightest evidence of fusion." Without in any way disagreeing with the first part of this statement, it may be pointed out that from the developmental point of view the morphology of the panicle represents the crux of the problem; namely, by what developmental process is the simple alternate (distichous) arrangement of primordia, as seen in the basal vegetative portion of the shoot, transformed into the polystichous arrangement found in the apical reproductive region.

(3) Bonnett's developmental studies have shown that the florets of both male and female inflorescences are potentially hermaphrodite. What factors determine

---

<sup>1</sup>Now at Department of Agronomy, Texas Agricultural Experiment Station, College Station, Texas.

whether the anthers shall degenerate leaving a pistillate inflorescence in the ear, or the pistil degenerate leaving functionally male flowers in the tassel?

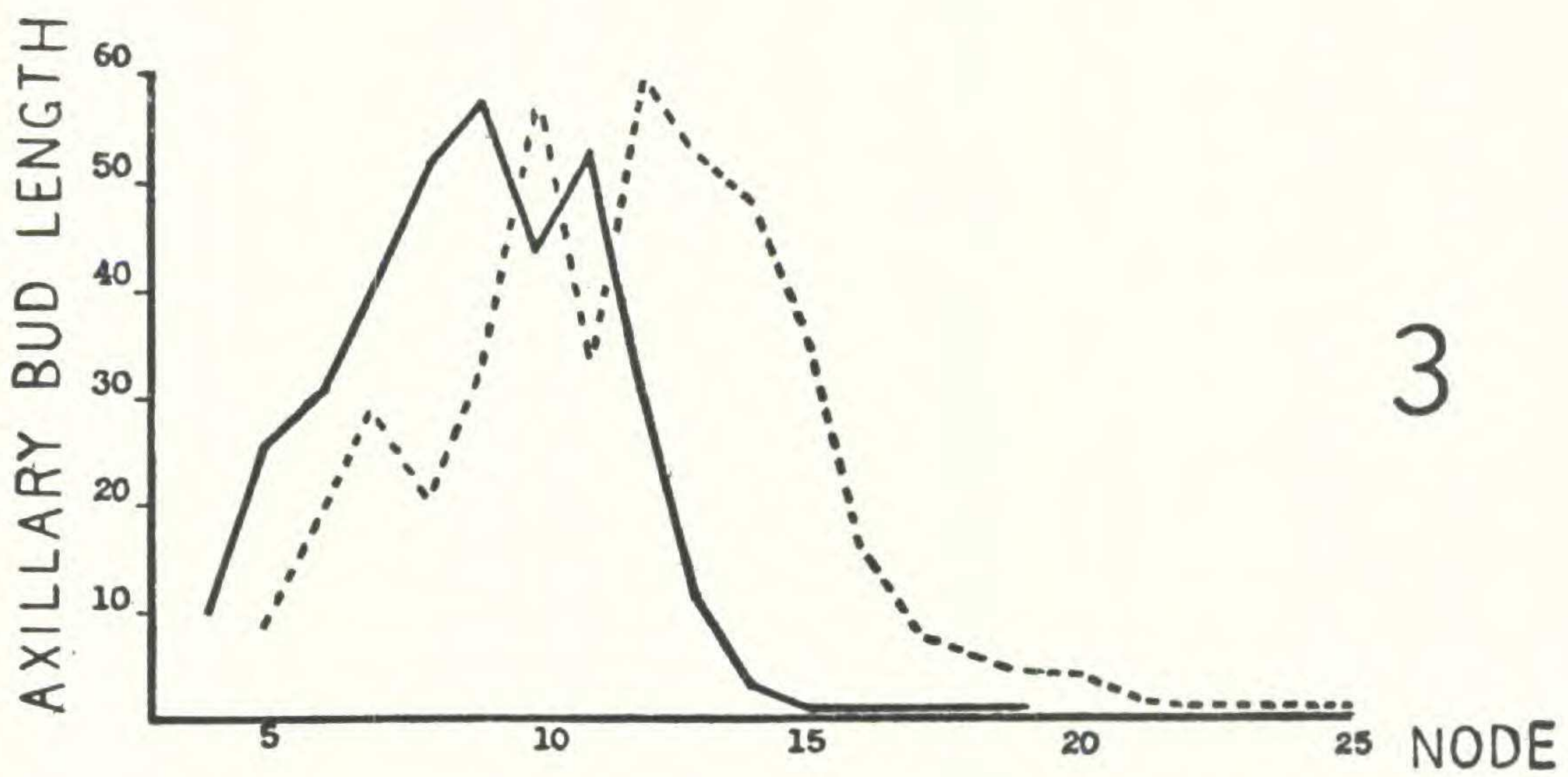
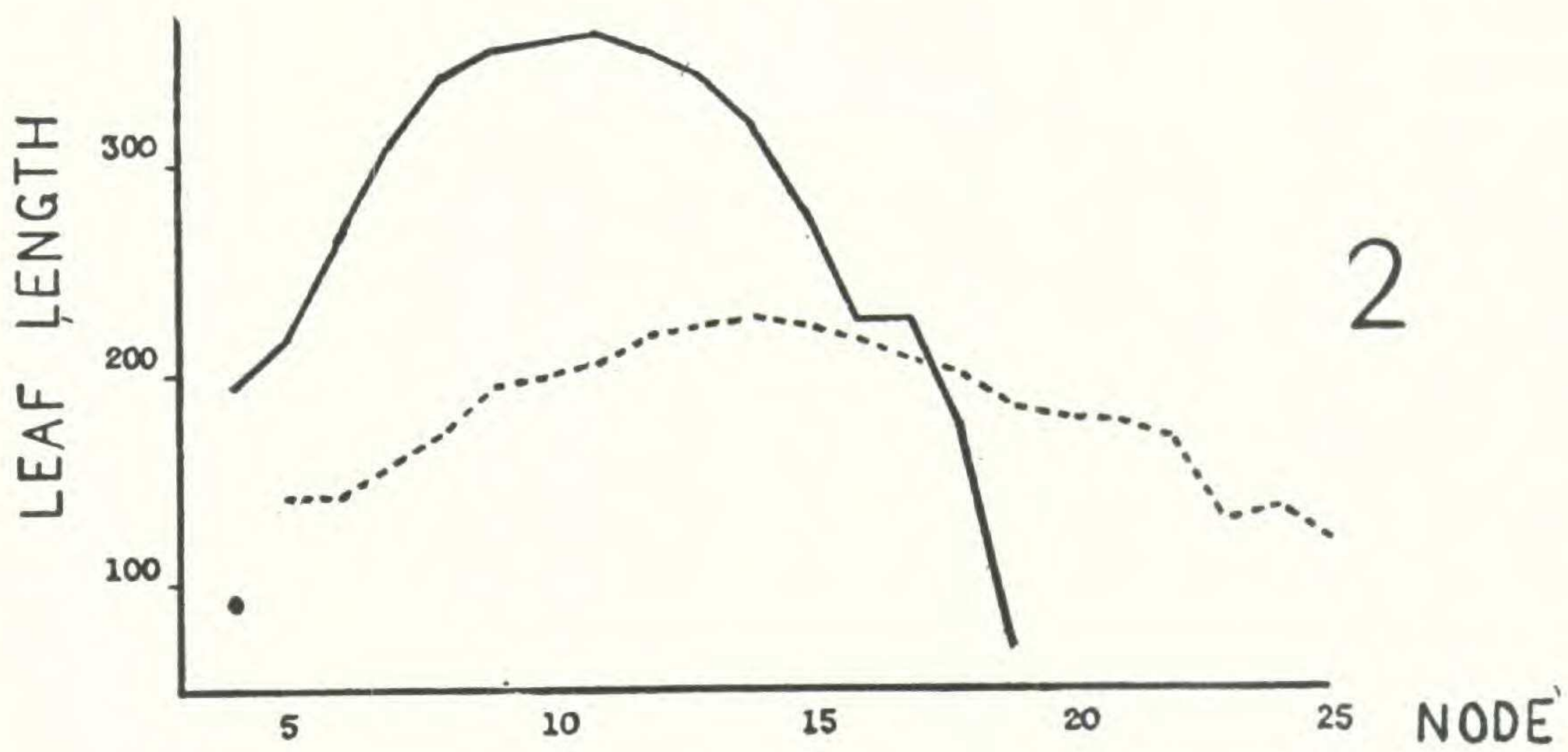
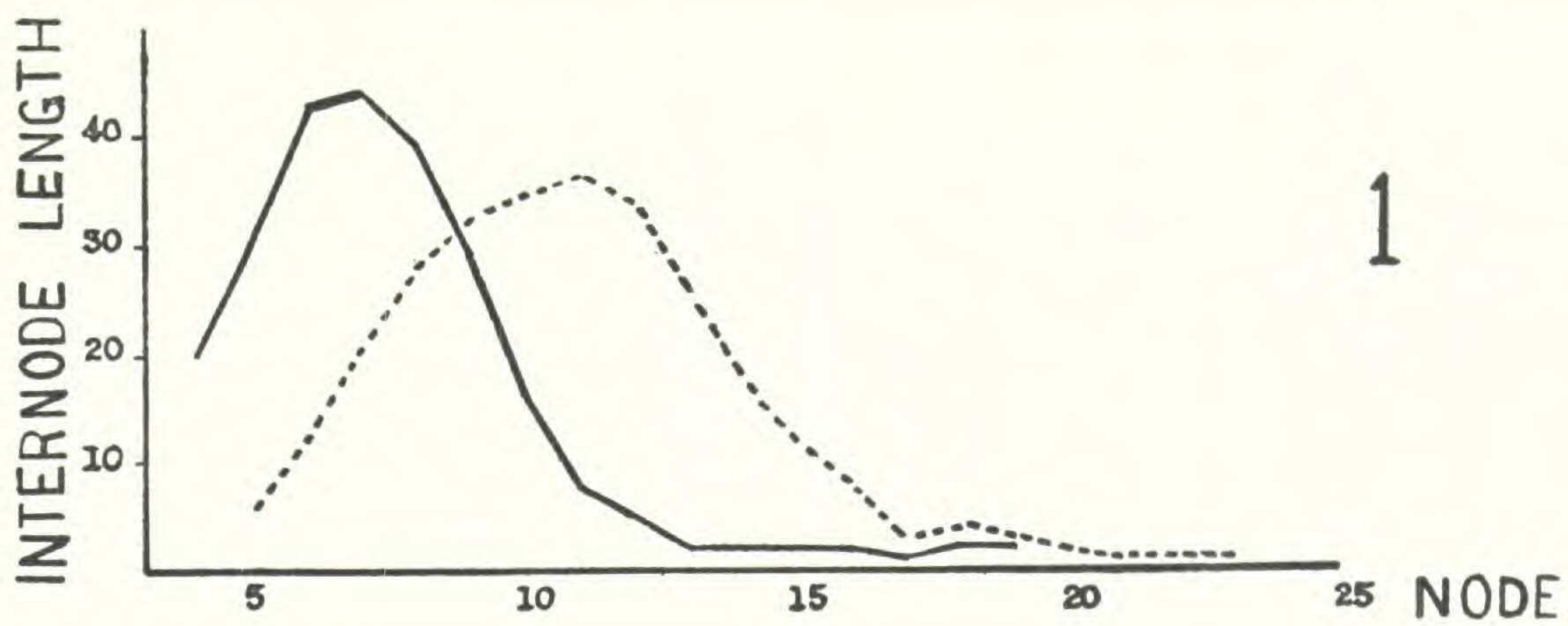
The writer's interest in these problems was first aroused by Dr. Edgar Anderson, who suggested that the disturbances in the normal pattern of development which are found in certain dwarf mutants in maize might be of value in interpreting ear and tassel morphology. A dwarf mutant which occurred as a simple recessive in one of her inbred strains was kindly handed over to the writer for study by Dr. Barbara McClintock. It is the purpose of this paper to report the results of a preliminary comparative study of this mutant and its normal sib, which are believed to have some bearing on the interpretation of tassel and ear morphology.

#### COMPARISON OF THE DEVELOPMENTAL PATTERN IN NORMAL AND DWARF PLANTS

The dwarf mutant segregated out as a simple recessive from a strain, B 97(1). Spontaneous chromosome breakage had occurred in this same strain but the particular line considered in this paper was cytologically normal. In 1945 two plantings of a line heterozygous for the mutant were carried out; the first in March and the second in June. Mutants and normal sibs were therefore available for developmental comparison from the two plantings.

*First planting.*—It was possible to distinguish mutant plants in the 6–8 leaf stage, as the leaves were shorter and narrower than in normal plants and tended to project at right angles from the main axis. At a later stage the shorter internodes, with the edges of each leaf sheath closely overlapping its neighbor, gave the plant a sort of "cross-gartered" appearance. Tassel emergence occurred at about the same time as in the normal sibs, but owing to the crowded internodes in the mutant, the tassel was never fully exerted above the topmost leaf sheath. Ear shoots were produced later (i.e. at higher nodes) than in the normal sibs, so that the general picture when the silks emerged was a dwarf plant, about half the normal height, with compressed internodes and the upper leaves, ears, and tassel all bunched together at the apex. The clubbed appearance was accentuated by the fact that in no case did the mutant plants tiller, in contrast to the normal sibs which produced 1–3 tillers.

At tassel emergence three normal and three mutant plants were dissected into their component leaves, axillary shoots, and main stem. Measurements of leaf lengths, internode lengths, and lengths of axillary buds were carried out. The first distinguishable node at the base of the stem was considered Node 1, and on this basis average measurements for corresponding parts were determined for normal and mutant plants. A general picture of the course of development during the vegetative phase was obtained by plotting these average values against their corresponding node numbers as shown in figs. 1, 2 and 3. Although the measurements represent averages of only three plants, the curves obtained are relatively smooth and are deemed adequate for illustrative purposes.



Figs. 1-3. Comparative dimensions of normal and mutant plants at time of tassel emergence as shown by internode lengths (fig. 1), leaf lengths (fig. 2), and lengths of axillary buds (fig. 3), associated with successive nodes of the main axis. Normal shown by solid, mutant by broken line.

Examination of the figures shows that in all cases there is a peak in vegetative vigor as measured by size of parts. Internodes, leaves, and axillary buds become progressively larger during the course of development and then decrease in size towards the apex of the shoot. The stage at which the peak occurs is probably associated with the beginning of the reproductive phase, since dissection of young normal plants when 10–12 leaves had been exerted usually showed tassels in the earliest stages of differentiation (c.f. Bonnett, 1940). The largest axillary buds (fig. 3) mark the position of the future ears. In the case of both normal and mutant plants the peak is reached first in internode length, second in length of axillary bud, and third in leaf length. This sequence agrees with Sharman's (1942) detailed studies which showed that during development a "wave of maturation" commences at the tip of each lamina and passes downward through the sheath and internode below. Maximum length should therefore be attained earliest in the lamina and latest in the internode.

Comparison of the data for normal and mutant plants shows that for the three series of measurements shown in the figures, the vegetative peak is reached at a later node in the mutant. At tassel exertion the mutant has produced more nodes and therefore, also, more axillary buds with subtending leaves. Internodes and leaves are shorter in the mutant than in the normal plant at a corresponding stage, though axillary buds appear to be similar in size. In general, the effect of the mutant gene appears to be a disturbance of the normal pattern of development such that the nodes are differentiated more rapidly, but the growth of associated structures (leaves, axillary buds, internodes) is markedly reduced.

*Second planting.*—No essential differences from the first planting were noticed during the early stages of growth. As before, mutant plants could easily be distinguished from their normal sibs. At tassel exertion, however, a striking effect of the late planting conditions was manifested by both mutant and normal plants. In the earlier planted material neither mutants nor normal plants had shown any abnormality in tassel or ear characters. In the mutant, the ears were crowded in the upper leaf axils around the tassel but they were structurally normal. By contrast, at the second planting, while the main axis tassels of "normal" plants were always structurally normal, nearly all the tillers had tassels partially modified towards femaleness. The degree of modification varied considerably; in extreme cases the whole central axis of the tassel was converted into an ear, the laterals remaining staminate, while in milder cases only a few spikelets at the base of the tassel were pistillate. Such partial sex reversal in tillers is not uncommon in certain strains of corn, and is the general rule in others, but the strain under investigation had shown no trace of such a tendency at the earlier planting. It is probable that the environmental factors responsible were either the short day length or cold night temperatures occasioned by the late planting, since both these factors are known to modify the phenotype considerably (Purvis and Gregory, 1937; Went, 1944).

In the case of mutant plants no tillers were produced and dwarfing was more pronounced than at the earlier planting. Dissection showed that the uppermost nodes were extremely crowded, and always telescoped into each other to some extent (pl. 32A). As a result of this crowding the zone of nodes bearing no axillary buds, which normally exists between the uppermost ear-bearing node and the base of the tassel, was almost completely eliminated. Instead, there existed a continuous series of lateral branches, the lowermost members of which were normal ears borne in the leaf axils, and the uppermost members were paired spikelets arising directly on the main axis with no subtending leaf. Between these extremes a continuous graded series could be arranged which is illustrated in plate 32B. The top row from left to right in the plate represents branches borne in the axils of the upper leaves at progressively younger (higher) nodes. The first member of the series does not differ essentially from the normal ears borne at lower nodes, although the ear is very small and the sheathing husks reduced to two. The rest of the series shows a progressive conversion of the ear into a structure indistinguishable from a lateral tassel branch except for a single reduced "husk" at the base. The lower row in the plate shows a continuation of the series, representing lateral branches which occurred above the topmost leaf, i.e. they had no subtending leaf. This continuation of the series shows a graduation from a lateral tassel branch to a paired spikelet borne on the main axis.

Since the effect of the mutant gene at the earlier planting was to crowd the ear-bearing nodes towards the tassel (fig. 3) as compared with the normal plant, its effect at the later planting may be regarded as a more extreme expression of the same process. Here the crowding has been so great that the normally clear-cut sequence—ear-bearing nodes, nodes with no axillary buds, lateral tassel branches—has been condensed so that an intergrading series from ear to lateral tassel branch is the result.

#### DISCUSSION

*The homology of lateral primordia in cereals.*—The work of Purvis and Gregory (1937) on the vernalization of winter rye showed that double primordial ridges, occurring at the lower nodes of the main axis in the early stages of development, and the spikelet initials, found at the apex of the shoot, are homologous structures. Towards the base of the shoot the lower ridge in each double primordium develops into a foliage leaf, while at the upper nodes the lower ridge fails to develop and the upper ridge forms a pair of spikelets. The node at which the switch from leaf-forming to spikelet-forming primordium takes place could be varied experimentally by low temperature pre-treatment and also by variation in day length. That this developmental plan is common to all cereals seems likely. Bonnett's developmental studies (*loc. cit.*) of the inflorescences of wheat, barley and oats, showed that at the beginning of differentiation each spikelet is subtended by a lower ridge, which he interpreted as being homologous with the foliage leaves

borne at the lower nodes. In maize he noted that only the female inflorescence showed these subtending ridges. Certain species of barley regularly have their lower spikelets enclosed by large leaf-like structures, clearly homologous with the leaves borne at lower nodes. Occasionally, too, in oats an aberrant plant occurs in which a structure indistinguishable from a lateral panicle branch is borne in the axil of the topmost leaf sheath. Sharman (1942) concluded that the subtending leaf and the axillary bud occurring at each node of the shoot are botanically unrelated structures, the former being anatomically associated with the internode below, and the latter with the internode above. However, whether it is more correct to think of double primordia, or two distinct initials which are always borne in juxtaposition, does not affect the main issue—the homology of tassel branches and axillary buds (ear-shoots). The mutant described in this paper, which exhibits a continuous range of expression from axillary ear shoot to lateral tassel branch, provides developmental evidence of the correctness of the anatomical theory.

Since tassel branches and axillary buds (ear shoots) are homologous, they must represent different stages in a developmental series and it might be expected that the developmental processes which have operated in forming the tassel would leave traces in axillary buds, i.e. in ear shoots and tillers. This expectation is supported by Anderson's discovery (1944) that degree of condensation of the lateral tassel branches is strongly correlated with the number of rows in the ear. It would seem that where an unbroken series of primordia can be induced to develop, as in the mutant described here, it should be possible to distinguish acropetal gradients in the processes affecting the development of the inflorescence. These may be considered in relation to the three questions suggested in the introduction of this paper.

*Reduction of lateral branches.*—Reference to pl. 32B shows that in passing from lower to upper nodes, i.e. from ear-bearing nodes to nodes bearing paired male spikelets, there is a gradual decrease in the number of parts borne by the axillary branches. This begins as a reduction in the number and size of the husks enclosing the lateral branch (see top row) and continues as a reduction in the number of spikelets (see bottom row). In the normal maize plant this progressive series is broken, because the intermediate stages are suppressed (there is a zone of nodes between the topmost ear-bearing node and the node bearing the lowermost tassel branch, which carries no axillary buds). The disturbance in normal development exhibited by the dwarf mutant eliminates the sterile zone and in doing so clearly demonstrates that reduction in spikelet number in passing from base to tip of the main axis of the tassel is but a continuation of a process initiated earlier in the vegetative parts of the plant.

*Condensation of nodes.*—Condensed nodes were frequently found in the main axis of mutant plants, an example of which is illustrated in pl. 32A. In this illustration the number of leaves borne at each "node" or condensed group of nodes is

indicated by the white figures. The lowest "node" shown in the illustration carried two leaves and it can be seen that the "node" really consists of two adjacent nodes with a very short internode between. The next "node" bore six leaves, which suggested that it consisted of a complex of at least six nodes, though only two nodes joined by a spiral ridge are visible externally. The four higher "nodes" bore no leaves and appear to be simple, but the fact that they bore three, five, and five lateral branches respectively, throws doubt on their apparently simple structure and suggests rather that each "node" is in reality a complex of several nodes.

Other evidence of condensation is illustrated in pl. 33. The leftmost picture (a) shows a portion of a tiller of a normal plant which bore a tassel partly modified towards femaleness (tassel-ear). Examination of many such tassel-ears showed evidence of node condensation. Next in order from left to right (b) in pl. 33 is a portion of an axillary branch which developed at a node below the usual ear-bearing region in a normal plant. This branch was induced to develop by extirpating the main axis tassel at an early stage of development. Although a normal ear was borne by this branch, the shank is greatly elongated and structurally similar to a tassel-bearing tiller, but shows condensation of nodes. The two rightmost illustrations (c) and (d) from normal plants show ears borne on long shanks which again show node condensation. In the case of all four branches illustrated in the plate, the nodes below the condensed region bore only one leaf per node, but above the condensed region, more leaves than visible nodes were always present. *This condition would seem to be true for normal ear-bearing branches in general, since careful examination shows that the number of husks enclosing the ear is always greater than the number of distinct ridges on which they are borne.*

It seems to the writer that the association of the ear structure with a region of condensed shank nodes immediately below it may be of developmental significance. Examination of many condensed regions similar to those illustrated in pl. 33 suggests that condensation begins with a twisting of the axis. If the twisting is severe, the node becomes tilted to one side and fused with the node immediately below. In other words, the series of separate ridges becomes converted into a continuous helical ridge. Further twisting results in a suppression of the internode between the gyres and a consequent fusion of neighboring gyres. When neighboring gyres are fused a multiplication of axillary structures (leaves and axillary buds) results. The stages leading to this multiplication can only be recognized in suitable material like that illustrated in pl. 33, but it may be suggested that an acceleration of the same process underlies the multiplication of spikelets in both ear and main axis of the tassel. If this interpretation is correct, the "nodes" of the male and female inflorescences which exhibit a polystichous arrangement of spikelets represent complexes of nodes, each sub-unit of which bears two spikelets. The condensation initiated in the shank would be continued and intensified in the ear itself. The normal tassel, since no leaves subtend the lateral branches, provides no

clue as to its complex nature, but the same underlying structure seems evident from the condensation exhibited by the abnormal mutant tassel illustrated in pl. 32A. Furthermore, this interpretation appears to be the simplest way of explaining the correlation between degree of tassel condensation and ear row number which has been demonstrated by Anderson (1944).

It might be argued that the chance fusion of nodes with accompanying multiplication of parts could only produce an irregular arrangement of spikelets in the inflorescence, whereas the row number found in the ear is a very regular and constant feature. This, however, would ignore the obvious, though little understood, laws of organized development which underlie phyllotaxy. The mechanical precision with which repeated structures are arranged in relation to one another has been stressed by Thompson (1942). He has shown that diverse problems of phyllotaxy may be interpreted, though not explained, in terms of rather simple mathematical constants. Thus the position of an axillary bud, pair of spikelets or leaf, appears to pre-determine or (in the mathematical sense) generate the position of the corresponding structure at the succeeding node. In a perfect alternate distichous arrangement, one structure generates the position of the next at an angle of  $180^\circ$  in respect to the main axis. If the angle is a little more or a little less than  $180^\circ$  a helical twist is superimposed on the distichous arrangement, as can often be seen in the arrangement of leaves on a young maize plant. Now, if two nodes become fused, it would appear that each pair of spikelets would act as independent generators in the production of spikelet pairs at the succeeding node, and this process might be expected to continue in an orderly fashion without further fusion of nodes. In short, a 16-row ear does not require a repeated fusion of nodes in groups of eight, but merely that eight nodes shall be condensed *once*, and that the eight spikelet pairs shall each generate a spikelet pair at successive nodes. Since an apparent fusion of six nodes can be seen in the abnormal tassel shown in pl. 32A, fusion of this order would not appear to make undue demands on the anatomical structure of the axis. It may be noted that the mechanisms suggested would be applicable to panicles in general, and not confined to the maize inflorescence.

If condensation of nodes is the explanation of the change from a distichous to a polystichous condition, there would appear to be a gradient of increasing condensation from the base to the apex of the main axis, and from the base to the apex of all axillary branches, i.e. in the tassel from the lower distichous lateral branches to the upper polystichous central axis; in the ear shoot from the lower nodes in the shank bearing distichous sheathing husks to the upper spikelet bearing nodes which are all polystichous. Normally, condensation is synchronized rather closely with the switch from vegetative primordium to spikelet initial, but when the synchronization is disturbed, either by environmental effects or by mutation which modifies the normal growth processes, as in the mutant described here, the mechanism of condensation can be observed in the vegetative phase of development.



*The determination of maleness and femaleness.*—The material considered in this paper sheds little light on the mechanism which determines whether male or female spikelets shall be produced. Within the restricted limits of the material examined, however, the following generalizations appear to be valid:

- (1) An axillary branch bearing an inflorescence which exhibits a greater or less degree of femaleness is usually associated with obvious condensation in its lower, leaf-bearing nodes.
- (2) In inflorescences of mixed sex, it is the more condensed nodes which tend to bear female spikelets. Thus it is usual for the central condensed axis of a tassel-ear to bear female spikelets; the lateral, less condensed tassel branches are preponderantly male.
- (3) Tillers (i.e. axillary branches which develop independent root systems) bear tassels or tassel-ears. Axillary branches, when induced to develop by tassel extirpation at nodes *below* the normal ear-bearing nodes and *above* the tillers, usually bear ear-shoots.
- (4) The inflorescence borne at the apex of the main axis and the inflorescence borne at the apex of a tiller are labile in respect to sex; the switch mechanism being affected by day length and/or thermoperiodicity.

#### SUMMARY

- (1) A comparative developmental analysis of a recessive dwarf mutant with its normal sib in maize suggests that the dwarfing gene: (a) increases the production of nodes and associated axillary structures; (b) reduces the lengths of the internodes, leaves and leaf sheaths; (c) delays the production of axillary ears so that the sterile zone, normally existing between the uppermost ear-bearing nodes and the lowest tassel branches, tends to be eliminated.
- (2) Under suitable conditions the axillary branches in the dwarf mutant exhibit a graded series, ranging from normal ear to paired male spikelets.
- (3) Within this graded series the following tendencies are evident:
  - (a) Progressive reduction in number and size of the lateral organs borne by the axillary branches in passing from base to apex of the main axis.
  - (b) Progressive condensation of nodes from base to apex both in the tassel and in ear-bearing axillary branch (shank).
  - (c) Association between degree of condensation and femaleness.
- (4) The observed tendencies are used to suggest a probable interpretation of the morphology of tassel and ear in the normal maize plant.

#### LITERATURE CITED

- Anderson, E. (1944). Homologies of the ear and tassel in *Zea Mays*. *Ann. Mo. Bot. Gard.* 31:325-340.
- Bonnett, O. T. (1935). The development of the barley spike. *Jour. Agr. Res.* 51:451-457.
- , (1936). The development of the wheat spike. *Ibid.* 53:445-451.
- , (1937). The development of the oat panicle. *Ibid.* 54:927-931.
- , (1940). Development of the staminate and pistillate inflorescence of sweet corn. *Ibid.* 60:25-37.

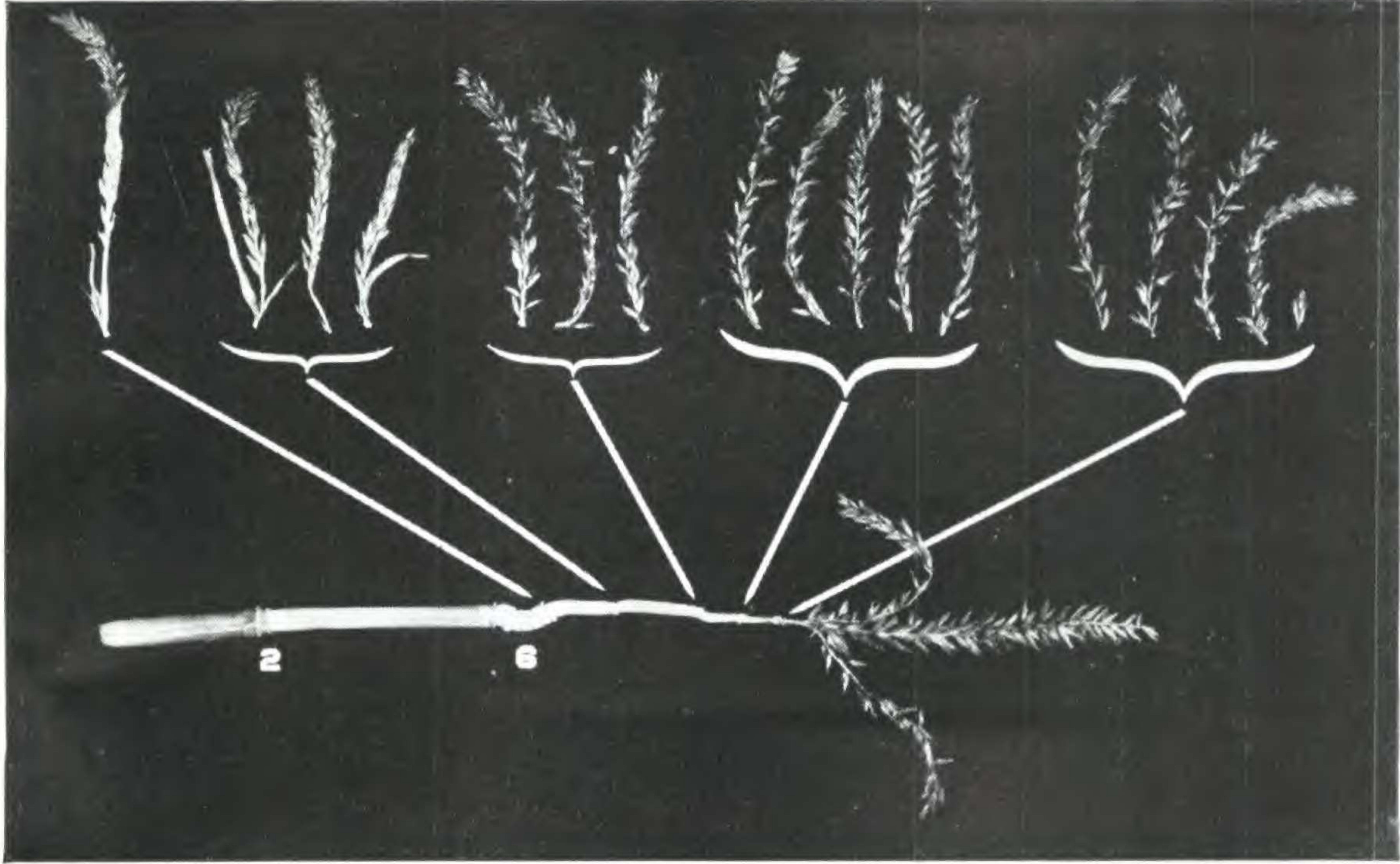
- Mangelsdorf, P. C. (1945). The origin and nature of the ear of maize. *Bot. Mus. Leafl. Harv. Univ.* 12:35-75.
- Purvis, O. N., and Gregory, F. G. (1937). Studies in vernalization of cereals. I. *Ann. Bot. (N.S.)* 1:569-591.
- Sharman, B. C. (1942). Developmental anatomy of the shoot of *Zea Mays* L. *Ibid.* 6:245-282.
- Thompson, D'Arcy W. (1942). *On growth and form*. 2nd ed. Cambridge University Press.
- Went, F. W. (1944). Plant growth under controlled conditions. II. *Am. Jour. Bot.* 31:135-150.

## EXPLANATION OF PLATE

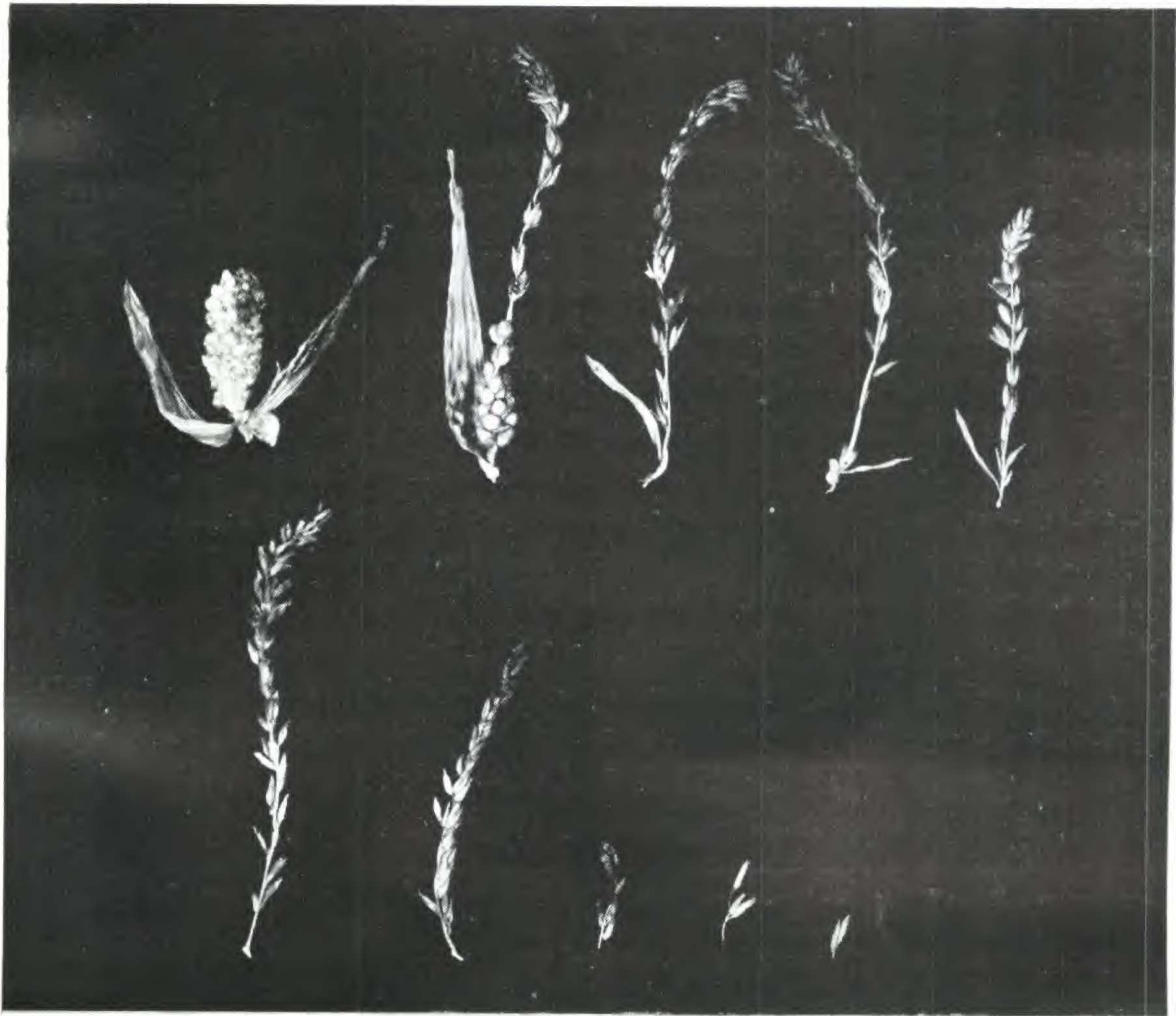
## PLATE 32

Fig. A. A dissected tassel and uppermost nodes of the main axis in a late-planted mutant. Figures indicate the number of leaves removed from each node; the position of the lateral branches is indicated by lines.

Fig. B. A range of lateral branches occurring in late-planted mutants, in a region corresponding to the sterile zone of the main axis in a normal plant. Upper row—lateral branches borne in the axils of foliage leaves; lower row—lateral tassel branches arising at nodes with no subtending leaves.



A



B

STEPHENS—TASSEL AND EAR OF DWARF MUTANT